

University of West Bohemia  
Faculty of Applied Sciences  
Department of Mathematics

# **BACHELOR THESIS**

## **Logistic Growth Model and its Modifications**

Pilsen 2012

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## **Declaration**

I hereby declare that this bachelor thesis is completely my own work and that I used only the cited sources.

Pilsen, \_\_\_\_\_

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signature



## **Acknowledgement**

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# Preface

The subject of this bachelor thesis is the logistic growth model and its modifications. The thesis is divided into two parts, focusing on deterministic and stochastic models, whereas in both cases a continuous-time or a discrete-time is considered.

The first part is focused on the deterministic logistic growth also known as logistic equation in continuous-time, and in discrete-time it is focused on the logistic map and its behaviour. The second part of the thesis describes stochastic population logistic growth models using discrete-time and continuous-time Markov chains.

The aim of this thesis is to present the models mentioned above, to summarize information obtained from the different sources and to compare the growth models.

**Keywords:** growth model, logistic growth model, deterministic growth model, stochastic growth model, logistic equation, logistic map, Cobweb diagram, Markov chain models, general process of growth, Yule process





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# Chapter 1

## Introduction

Mathematical model is a description of a system which may help to explain the system, make predictions about its behaviour and to study effects of different components. Mathematical models are used mostly in the natural sciences and engineering but also in the social sciences such as economics<sup>1</sup>.

Deterministic models are mathematical models which contains no random elements and completely determine  $y$  if  $x$  is known, that is why they are called deterministic. Since they are closely associated with differential equations, they began to be widely used with their development by mathematicians such as Jakob Bernoulli, Johann Bernoulli, and Leonhard Euler in the early 18th century to study physical processes.[8]

Stochastic models are often used to establish and represent the evolution of some random variable over time. In general, its application started in physics and now it is applied in engineering, life sciences, social sciences, and finance<sup>2</sup>. Although it may seem that the processes of growth are not very important compared to birth death processes they have great significance for investigation of epidemics, diseases, viruses and bacteria diffusion. These processes can be also applied to population studies and their uncontrolled growth. It has been a problem since the late 1960s and the early 1970s where the population of the Earth achieves four milliards (in 1830 it was one milliard, 1930 two milliards, 1960 three milliards and 1975 four milliards). This problem can be found especially in developing countries, for example in India.[4]

In Chapter 2 we focus on deterministic models. In the Section 2.1 we present logistic growth (logistic equation) published by Pierre-François Verhulst in 1838 (more information about Verhulst and his work are in Chapter 6 in book [2] written by N. Bacaër). Detailed information about this equation and its modifications can be found in books written by J.D. Murray [10] and by R.B. Banks [3]. In Section 2.2 we describe how it is possible to get the discrete-time model from the continuous-time logistic equation defined in the previous section. Various types of discretization and the obtained models are described by P. Turchin in his book [14]. We obtain the well known logistic map and describe and simulate its behaviour.

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<sup>1</sup>[http://en.wikipedia.org/wiki/Mathematical\\_model](http://en.wikipedia.org/wiki/Mathematical_model)

<sup>2</sup>[http://en.wikipedia.org/wiki/Stochastic\\_modelling\\_\(insurance\)](http://en.wikipedia.org/wiki/Stochastic_modelling_(insurance))

Chapter 3 is devoted to the stochastic growth models. In Section 3.1 we are dealing with continuous-time Markov chain models, in particular with a general process of growth. Basic information about Markov chain models can be found in [11] written by Prášková and Lachout. In this section we determine the transition rate matrix which is necessary for simulation, the stationary distribution and then we show two possibilities how to compute absolute probabilities. Finally we simulate stochastic logistic growth model. Simulation of the logistic growth based on the death and birth process can be found in the bachelor thesis [6] written by Vojtěch Kulhavý. In the next section we are dealing with the same general process of growth, only this time we consider it to be discrete-time Markov chain model. We determine its transition matrix and simulate this model. Information about stochastic birth and death process containing discrete-time and continuous-time Markov chain model and more are in the article [1] written by L.J.S. Allen and E.J. Allen.

In the last Chapter we summarize basic characteristics, advantages and disadvantages of the presented models and compare stochastic and deterministic models.

The aim of this thesis is to introduce growth models mentioned above, summarize the information obtained from the different sources and do simulations.

## Chapter 2

# Deterministic Growth Models

Deterministic models are mathematical models in which outcomes are precisely determined through known relationships among states and events, without any room for random variation. In such models, a given input will always produce the same output<sup>1</sup>.

In this chapter we use books *Mathematical Biology I., An Introduction* [10] written by J.D. Murray and *Complex population dynamics: a theoretical/empirical synthesis* [14] written by P. Turchin. Another used sources are lecture notes [7], [9], [12] and [13].

### 2.1 Continuous-time Models

Let  $N = N(t)$  be a population size (or its density) at time  $t$ . Then the rate of change

$$\frac{dN}{dt} = \text{births} - \text{deaths} + \text{migration}, \quad (2.1)$$

is a conservation equation for the population. In the simplest model there is no migration and the birth and death terms are proportional to  $N$ . That is,

$$\frac{dN}{dt} = bN - dN, \quad (2.2)$$

where birth and death coefficients  $b$  and  $d$  are positive constants and the initial population  $N(0) = N_0$ . The solution of (2.2) is a function  $N(t) = N_0 e^{(b-d)t}$ . Thus if  $b > d$  the population grows exponentially while if  $b < d$  it dies out. Obviously this linear model is very simple because the population growth doesn't depend on  $N$ . (More detailed information can be found in Section 1.1. in book [10] written by J.D. Murray.)

#### 2.1.1 Logistic Growth

Eventually there must be some adjustment to such exponential growth. Verhulst (1838, 1845; more in Chapter 6 in [2]) proposed that a self-limiting process should operate

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<sup>1</sup><http://www.businessdictionary.com/definition/deterministic-model.html>

when a population becomes too large and suggested the following differential equation for the population  $N(t)$  at time  $t$ :

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), \quad (2.3)$$

where  $r$  and  $K$  are positive constants,  $r$  is called *intrinsic growth rate* and  $K$  is the *carrying capacity* of the environment, which is usually determined by the available sustaining resources. In this model the per capita birth rate is  $r(1 - \frac{N}{K})$  so it is dependent on  $N$  (see Section 1.1. in [10]).

Let us first take a look at general properties of the logistic growth model. This ordinary differential equation (ODE) is non-linear thus in general it is not necessarily analytically tractable. Fortunately we can solve this simple non-linear ODE but even without the result we can heuristically explore the behaviour of the solution as follows.

From the logistic equation (2.3) we see that  $dN/dt$  is positive when  $N$  is close to zero but positive. This means that  $N$  is increasing at this position as time passes and this increase continues as long as  $N < K$ . We thus expect that the population size  $N$  approaches  $K$  upward. On the other hand, the time derivative is negative when  $N$  lies at a position above  $K$  and  $N$  is decreasing as time advances. This time we expect  $N$  approaches  $K$  downward. This consideration suggests that starting from any positive initial position  $N(0) > 0$ ,  $N$  will converge to  $K$ . Now we can see why  $K$  is called the carrying capacity, it is the limit of the environment where the population in focus occurs. Large  $K$  implies the environment can support a dense population ([13], Chapter 1).

Further we can see that there are two steady states, namely  $N = 0$  and  $N = K$  (that is, where  $\frac{dN}{dt} = 0$ ).  $N = 0$  is unstable since linearization about it (when initial population size is positive and very small,  $N \ll 1$ ,  $N^2$  is neglected compared with  $N$ ) gives

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) = rN - r\frac{N^2}{K} \approx rN(t). \quad (2.4)$$

This is an exponential grow and we see why  $r$  is called intrinsic growth rate, it is the rate of increase per individual in an ideal situation. The other equilibrium  $N = K$  is stable: linearization about it gives  $\frac{d(N-K)}{dt} \approx -r(N-K)$  and so  $N \rightarrow K$  as  $t \rightarrow \infty$  ([10], Section 1.1).

**Lemma 2.1.1.** *Solution of (2.3) with the initial condition  $N(0) = N_0$  is*

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}; \quad t \geq 0. \quad (2.5)$$

*Proof.* We use separation of variables to determine the solution from the equation (2.3). First we separate the variables

$$\frac{dN}{(1 - \frac{N}{K})N} = rdt. \quad (2.6)$$

Then we decompose the left hand side into partial fractions

$$\frac{dN}{K - N} + \frac{dN}{N} = rdt. \quad (2.7)$$



Next we integrate both the sides and rearrange the variables

$$\begin{aligned} \int \frac{dN}{K-N} + \int \frac{dN}{N} &= r \int dt \\ -\ln|K-N| + \ln|N| &= rt + c_1 \\ \left| \frac{N}{K-N} \right| &= c_2 e^{rt}. \end{aligned}$$

We rearrange this again, use the initial condition  $N_0$  and finally get the solution

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)}. \quad (2.8)$$

Since the derivative of  $N(t)$  is given by

$$N'(t) = \frac{N_0 K r e^{rt} (K - N_0)}{(K + N_0 (e^{rt} - 1))^2}, \quad (2.9)$$

it can be easily verified that  $N(t)$  is the solution.  $\square$

The following theorem from Section 1.1. in [7] summarize the properties of the logistic growth model.

**Proposition 2.1.2.** *The equation (2.3) has two steady states:  $N = 0$  and  $N = K$ . If  $N$  is an arbitrary solution of the equation (2.3) with  $N_0 > 0$ , then*

- (i)
  - $\lim_{t \rightarrow +\infty} N(t) = K$ ,
  - $\lim_{t \rightarrow +\infty} N'(t) = 0$ .

(ii) If  $N_0 \in (0, K)$ , then

- $N(t) \in (0, K), \forall t > 0$ ,
- $N'(t) > 0, \forall t > 0$ .

Moreover  $\exists t_0 \geq 0$  such that

- $N(t) \in (0, \frac{K}{2}), N''(t) > 0$  for  $t \in (0, t_0)$ ,
- $N(t) \in (\frac{K}{2}, K), N''(t) < 0$  for  $t > t_0$ .
- Specially if  $N_0 \in [\frac{K}{2}, K)$  then  $t_0 = 0$  and  $(0, t_0) = \emptyset$ .

(iii) If  $N_0 = K$ , then  $N(t) = K, \forall t > 0$ .

(iv) If  $N_0 > K$  then

- $N(t) > K, \forall t > 0$ ,
- $N'(t) < 0, \forall t > 0$ ,
- $N''(t) > 0, \forall t > 0$ .

*Proof.* (i) 

- We simply determine the limit from the exact solution (2.5)

$$\lim_{t \rightarrow \infty} N(t) = \lim_{t \rightarrow \infty} \frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)} = \lim_{t \rightarrow \infty} \frac{e^{rt} (N_0 K)}{e^{rt} (\frac{K}{e^{rt}} + N_0 - \frac{N_0}{e^{rt}})} = K. \quad (2.10)$$

- We determine the limit from the derivative (2.9)

$$\begin{aligned}\lim_{t \rightarrow \infty} N'(t) &= \lim_{t \rightarrow \infty} \frac{N_0 K r e^{rt} (K - N_0)}{(K - N_0)^2 + 2(K - N_0)N_0 e^{rt} + N_0 e^{2rt}} = \\ &= \lim_{t \rightarrow \infty} \frac{e^{rt} K N_0 r (K - N_0)}{e^{2rt} [e^{-2rt} (K - N_0)^2 + 2(K - N_0)N_0 e^{-rt} + N_0]} = 0.\end{aligned}$$

(ii) Suppose  $N_0 \in (0, K)$ .

- We can re-write it as  $0 < N_0 \wedge N_0 < K$ . We multiple the first inequality by  $\frac{K e^{rt}}{K + N_0 e^{rt} - N_0} (> 0)$  and get

$$0 < \frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)}. \quad (2.11)$$

Next we can subtract  $N_0$  and add  $N_0 e^{rt}$  to the second inequality

$$N_0 e^{rt} < K + N_0 e^{rt} - N_0 \quad (2.12)$$

and then multiply it by  $\frac{K}{K + N_0 (e^{rt} - 1)} (> 0)$ . We obtain

$$\frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)} < K. \quad (2.13)$$

We can see that  $0 < \frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)} \wedge \frac{N_0 K e^{rt}}{K + N_0 (e^{rt} - 1)} < K$ . We proved that if  $N_0 \in (0, K)$ , then  $N(t) \in (0, K)$ .

- Derivative (2.9) is positive, because denominator is always positive and numerator is positive because of the assumption.
- The second derivative of the exact solution (2.5) is

$$N''(t) = \frac{r^2 N_0 K e^{rt} (N_0 - K) (N_0 e^{rt} + N_0 - K)}{(K + N_0 (e^{rt} - 1))^3}. \quad (2.14)$$

We set this second derivative to zero to find the inflection point  $t_0$ . The fraction is equal to zero if the numerator is equation to zero (the denominator is positive)

$$r^2 N_0 K e^{rt_0} (N_0 - K) (N_0 e^{rt_0} + N_0 - K) = 0. \quad (2.15)$$

The equation is satisfied if

$$N_0 e^{rt_0} + N_0 - K = 0. \quad (2.16)$$

We can express  $t_0$  from this equation in the following form

$$t_0 = \frac{1}{r} \ln \frac{K - N_0}{N_0}. \quad (2.17)$$

Now we determine  $N(t_0)$ . We substitute  $t_0$  into equation (2.5) and do some rearrangement

$$\begin{aligned}N(t) &= \frac{N_0 K e^{r \frac{\ln \frac{K - N_0}{N_0}}{r}}}{K + N_0 (e^{r \frac{\ln \frac{K - N_0}{N_0}}{r}} - 1)} = \frac{N_0 K \frac{K - N_0}{N_0}}{K + N_0 (\frac{K - N_0}{N_0} - 1)} = \frac{K(K - N_0)}{2(K - N_0)} = \frac{K}{2}.\end{aligned} \quad (2.18)$$

We obtain function value of the inflection point  $t_0$ . Then the rest of the proof is obvious.

(iii) For  $N_0 = K$  we have that

$$N(t) = \frac{K^2 e^{rt}}{K + K(e^{rt} - 1)} = K, \forall t > 0. \quad (2.19)$$

(iv) Suppose  $N_0 > K$ .

- Assume  $N_0 = K + \epsilon > K$ . Then the exact solution  $N(t)$  (see equation (2.5)) will be in the following form

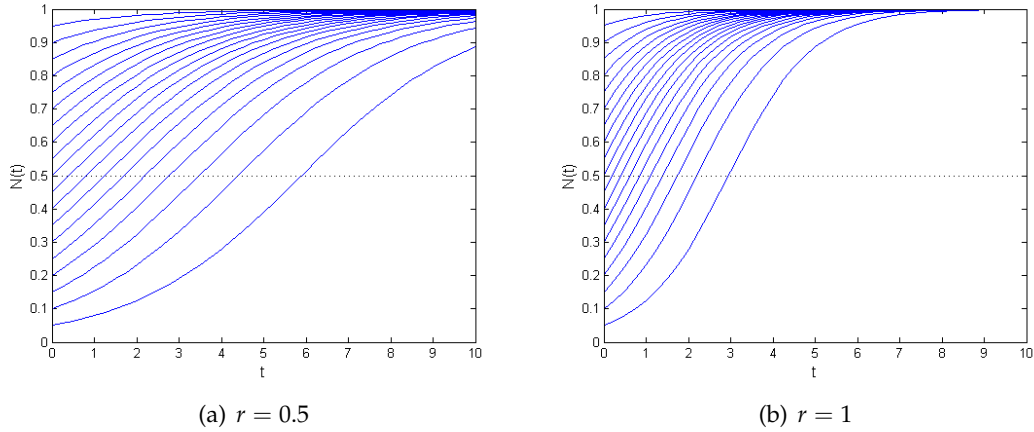
$$\frac{(K + \epsilon)Ke^{rt}}{K + (K + \epsilon)(e^{rt} - 1)} = \frac{K^2 e^{rt} + K\epsilon e^{rt}}{K + Ke^{rt} - K + \epsilon e^{rt} - \epsilon} = K \frac{e^{rt}(K + \epsilon)}{e^{rt}(K + \epsilon) - \epsilon} \quad (2.20)$$

which is always greater than  $K$ .

- Derivative (2.9) is negative, because denominator is always positive and numerator is negative because of the assumption.
- From the formula (2.14) it is obvious, that if  $N_0 > K$  then  $N''(t) > 0$ .

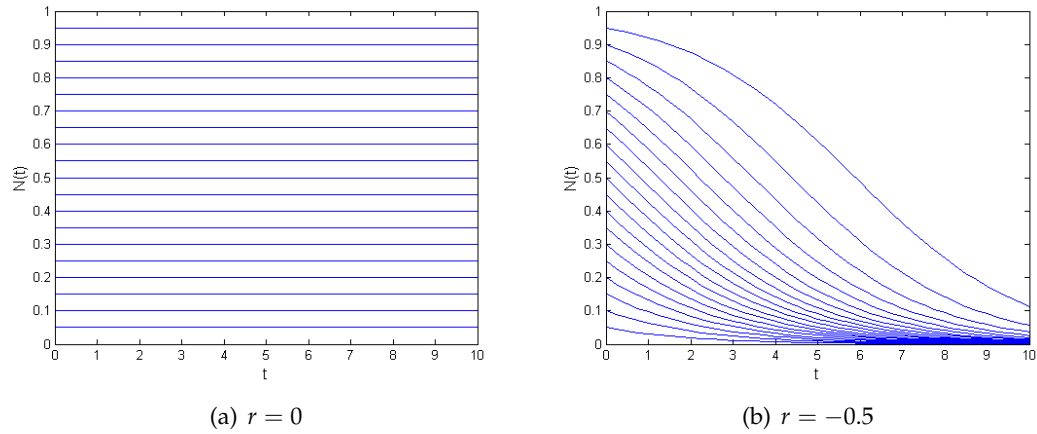
□

In Figure 2.1 we can see how is deterministic solution changed if we have  $r$  and  $K$  fixed and initial condition  $N_0$  is ranging from 0 to  $K$  in steps of 0.05. We can tell the solution is increasing if  $N_0 \in (0, K)$ , whereas it's convex until it reaches value  $\frac{K}{2}$  and concave since it gets over it. It means the population growth is slowing down since its density  $N(t)$  achieves the value  $\frac{K}{2}$ .



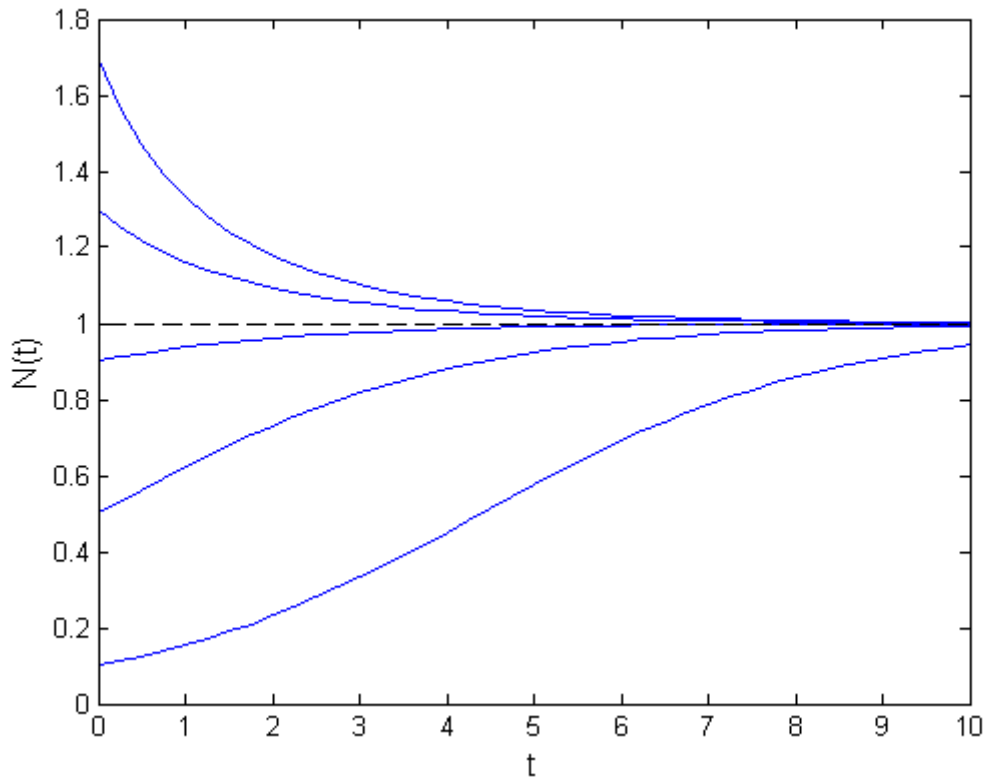
**Figure 2.1:** Logistic population growth for parameters  $K = 1$  and  $r > 0$  and different initial conditions  $N_0$ .

If  $r = 0$ , then the solution  $N(t) \equiv N_0, t \geq 0$ . If  $r < 0$ , then  $\lim_{t \rightarrow +\infty} N(t) = 0$ . Both these cases are illustrated in the Figure 2.2 below just for completeness, we cannot speak about a growth anymore.



**Figure 2.2:** Simulation of logistic equation for parameters  $K = 1$  and  $r \leq 0$ .

Also note that if  $N_0 > K$  then  $N(t)$  is decreasing as time advances and it approaches  $K$  downward (see Figure 2.3).



**Figure 2.3:** Simulation of logistic equation for parameters  $K = 1$  and  $r = 0.5$ ,  $N_0$  is ranging from 0.1 to 1.7 in steps of 0.4.

## 2.2 Discrete-time Models

Consider a time discretization  $0 \leq t_0 < t_1 < t_2 \dots; \Delta t_k = t_{k+1} - t_k$ . For simplicity let  $\Delta t_k \equiv \Delta t$ . There are at least three ways to discretize the continuous logistic model (equation). The first one is to discretize the derivative in the logistic model

$$\frac{\Delta N}{\Delta t} \approx \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \quad (2.21)$$

Let  $N_k = N(t_k)$  (we add subscript  $k$  to emphasize that we are now dealing with discrete-time density) and let  $\Delta N_k = N_{k+1} - N_k$ . By replacing  $\Delta N$  and  $\Delta t$  in equation (2.21) we obtain

$$N_{k+1} - N_k = rN_k\left(1 - \frac{N_k}{K}\right). \quad (2.22)$$

Then we adjust the equation

$$\begin{aligned} N_{k+1} &= N_k\left[r\left(1 - \frac{N_k}{K}\right) + 1\right] \\ N_{k+1} &= N_k\left[(r+1) - \frac{r}{K}N_k\right] \end{aligned}$$

and obtain the discrete logistic model, or better the logistic (quadratic) map

$$N_{k+1} = aN_k - bN_k^2, \quad (2.23)$$

where  $a = r + 1$  and  $b = \frac{r}{K}$ . This model is flawed for ecological application because if  $N_k$  happens to exceed  $K\frac{(1+r)}{r}$ , then at time  $k + 1$  population density  $N_{k+1}$  becomes negative ([14], Subsection 3.1.2). Nevertheless this is the most suitable model for running simulations.

The second derivation uses the following trick. We divide the logistic equation by  $N_k$  (again we add a subscript  $k$  to  $N$ )

$$\frac{\frac{dN}{dt}}{N_k} = r\left(1 - \frac{N_k}{K}\right), \quad (2.24)$$

substitute the left-hand side by the derivative of the natural logarithm  $(\ln N_t)'$

$$(\ln N_k)' = r\left(1 - \frac{N_k}{K}\right) \quad (2.25)$$

and replace it with  $N_{k+1} - N_k$ , we receive

$$\ln N_{k+1} - \ln N_k = r\left(1 - \frac{N_k}{K}\right) \quad (2.26)$$

which is

$$\frac{N_{k+1}}{N_k} = e^{r\left(1 - \frac{N_k}{K}\right)}. \quad (2.27)$$

Finally, we obtain the Ricker model

$$N_{k+1} = N_k e^{r\left(1 - \frac{N_k}{K}\right)}. \quad (2.28)$$

This model avoids the flaw of the logistic map: for any  $N_k > 0$  the model predicts a positive  $N_{k+1}$  ([14], Subsection 3.1.2).

The third way to discretize the continuous logistic model uses the analytical solution (2.5) of logistic equation. After rearranging the terms, substituting  $\lambda_0 = e^r$ , and switching to subscripts, as usual, we have

$$N_{k+1} = \frac{\lambda_0 N_k}{1 + [(\lambda_0 - 1)/k] N_k} \quad (2.29)$$

([14], Subsection 3.1.2).

### 2.2.1 Logistic Map

We discretized the continuous logistic equation and obtained the logistic (quadratic) map in the following form

$$N_{k+1} = aN_k - bN_k^2 = aN_k(1 - \frac{b}{a}N_k). \quad (2.30)$$

To simplify this equation, we let  $x_k = \frac{b}{a}N_k$ . Hence,

$$x_{k+1} = \mu x_k(1 - x_k), \quad (2.31)$$

where  $\mu$  (sometimes also denoted  $r$ ) is positive constant and  $x_i$  is the size of a population at time  $k$ . This one-dimensional non-linear map is also a population model which is capable of very interesting behaviour.

The solutions of the logistic map can exhibit surprisingly complex behaviour for some initial conditions and particular values of parameters. This behaviour can be so complex that it becomes impossible to predict the time evolution. Such behaviour is often called chaotic. In our case it depends on the value of  $\mu$  and there are many types of behaviour that can occur for different values of this parameter.

Before we investigate this behaviour, we introduce the method of determining the fixed points and their stability. The fixed point of a function is a value of  $x_k$  which gets mapped straight back to itself by the function. We can say that fixed point  $x^*$  of the function satisfies

$$x^* = f(x^*). \quad (2.32)$$

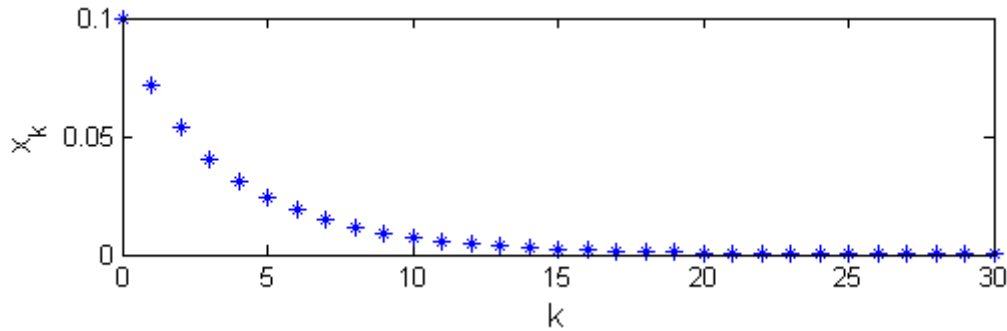
The analytic (or more precisely graphic) method of determining the fixed points and their local stability is called *cobweb diagram* method or cobwebbing [9]. Now, we describe its main principles.

Consider function  $f$  plotted on a set of axes. The  $x$ -axis represents  $x_k$  while the  $y$ -axis represents  $x_{k+1}$  so we obtain a phase diagram, in our case concave parabola. Then pick some starting point  $x_0$  on the  $x$ -axis. Starting from this point, we can find the next iterate of function,  $x_1 = f(x_0)$ , by drawing a vertical line to the plot. Then we mark  $x_1$  on the  $y$ -axis by drawing a horizontal line from the point of intersection. In order to find  $x_2 = f(x_1)$ , we need to move the point  $x_1$  marked on the  $y$ -axis to the same point on

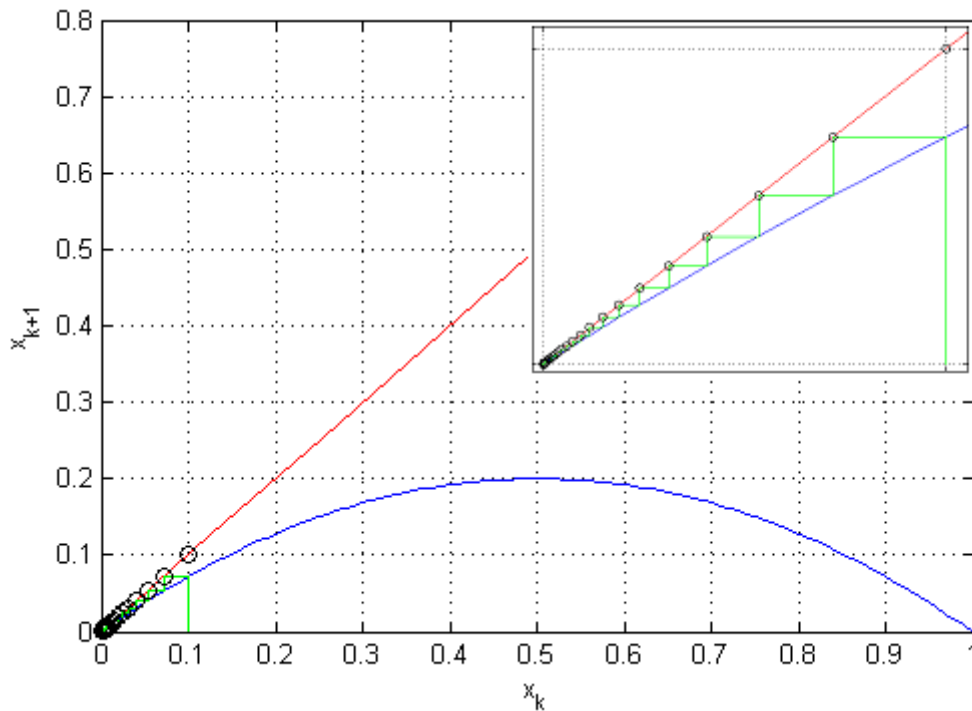
the  $x$ -axis. We do this by drawing the line  $y = x$  and finding the intersection of this line and the horizontal line  $y = x_1$ . Then we draw a vertical line down to  $x$ -axis and mark the point  $x_1$ . Now we have a new starting point  $x_1$  on the  $x$ -axis and by repeating the described procedure we obtain the next iteration  $x_2 = f(x_1)$ , then we repeat the process, until we generate the cobweb diagram ([12], Section 2.1).

At last, we can describe many types of behaviour of the logistic map that can occur for different values of this parameter  $\mu^2$  and illustrate it on the following graphs. (We have used a code<sup>3</sup> in software Matlab for simulation the cobweb diagrams.)

If  $0 < \mu < 1$ ,  $\mu$  is so low that population eventually dies, independent of the initial population size (see Figure 2.4 and 2.5).



**Figure 2.4:** Solution of the logistic map for  $\mu = 0.8$ .



**Figure 2.5:** Cobweb diagram for the logistic map for  $\mu = 0.8$ .

<sup>2</sup>[http://en.wikipedia.org/wiki/Logistic\\_map](http://en.wikipedia.org/wiki/Logistic_map)

<sup>3</sup><http://www.dam.brown.edu/people/cch/am136/Mfiles/cobweb.m>

If  $1 < \mu < 3$ , population approaches the value  $\frac{\mu-1}{\mu}$  (in the picture below,  $\frac{\mu-1}{\mu} = 0.375$ ) and becomes stable, independent of the initial population. For  $1 < \mu < 2$  it converges faster and quickly approaches the value (see Figure 2.6 and 2.1), for  $2 < \mu < 3$  it fluctuates around the value for some time (see Figure 2.8 and 2.9).

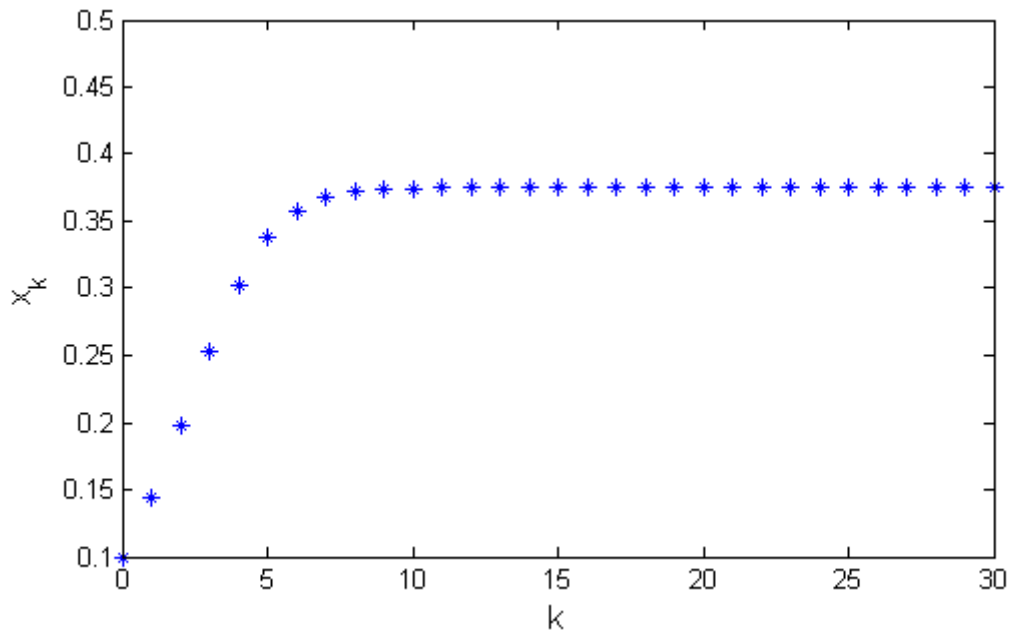


Figure 2.6: Solution of the logistic map for  $\mu = 1.6$ .

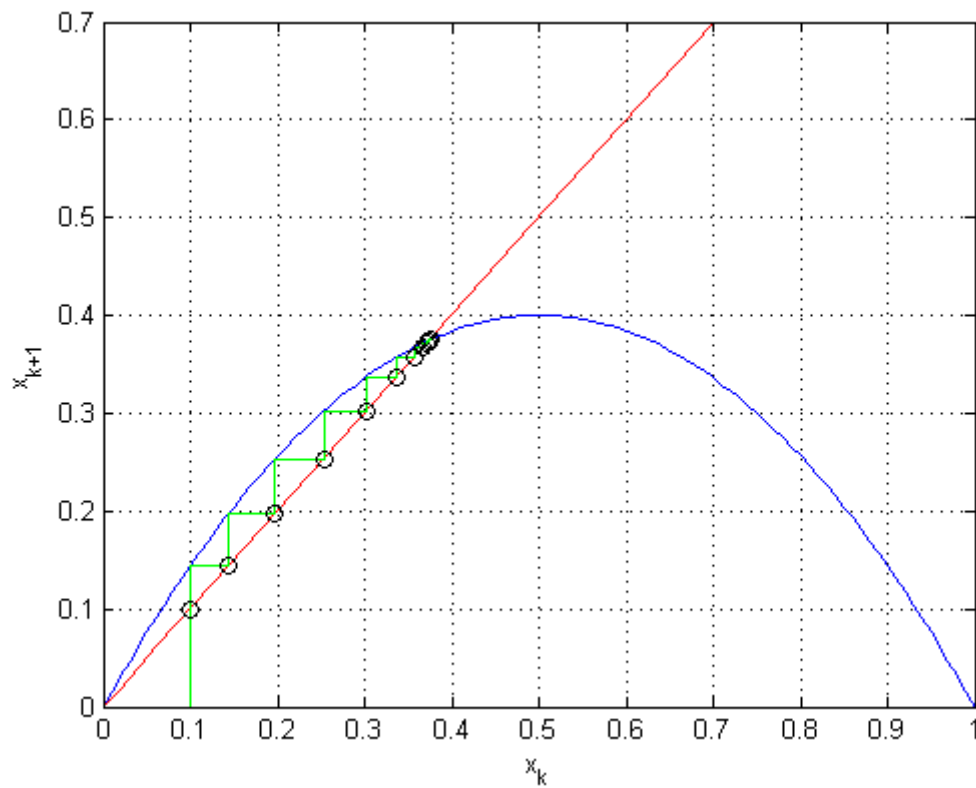
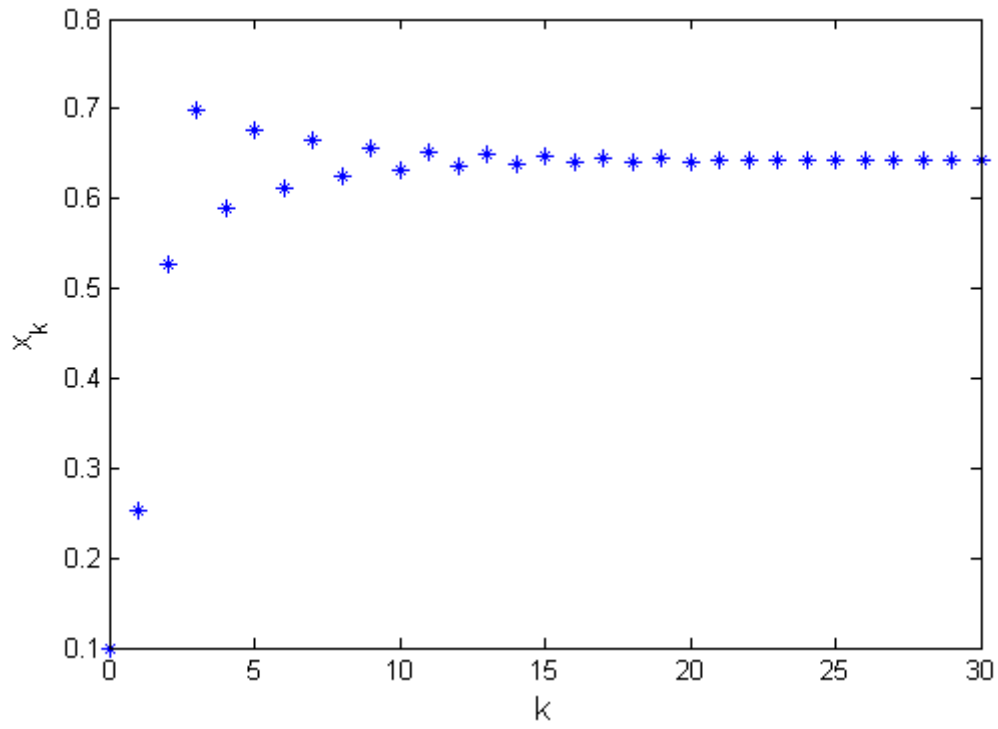
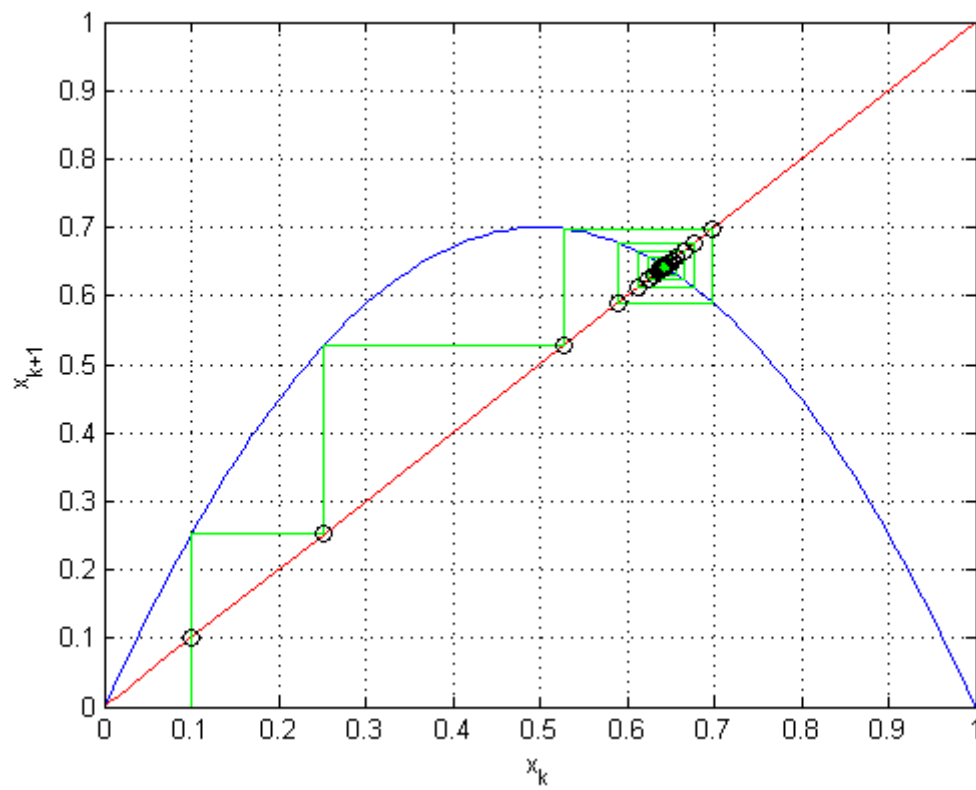


Figure 2.7: Cobweb diagram for the logistic map for  $\mu = 1.6$ .





**Figure 2.8:** Solution of the logistic map for  $\mu = 2.8$ .



**Figure 2.9:** Cobweb diagram for the logistic map for  $\mu = 2.8$ .

If  $3 < \mu < 1 + \sqrt{6}$ , population oscillates between two values (see Figure 2.10 and 2.11).

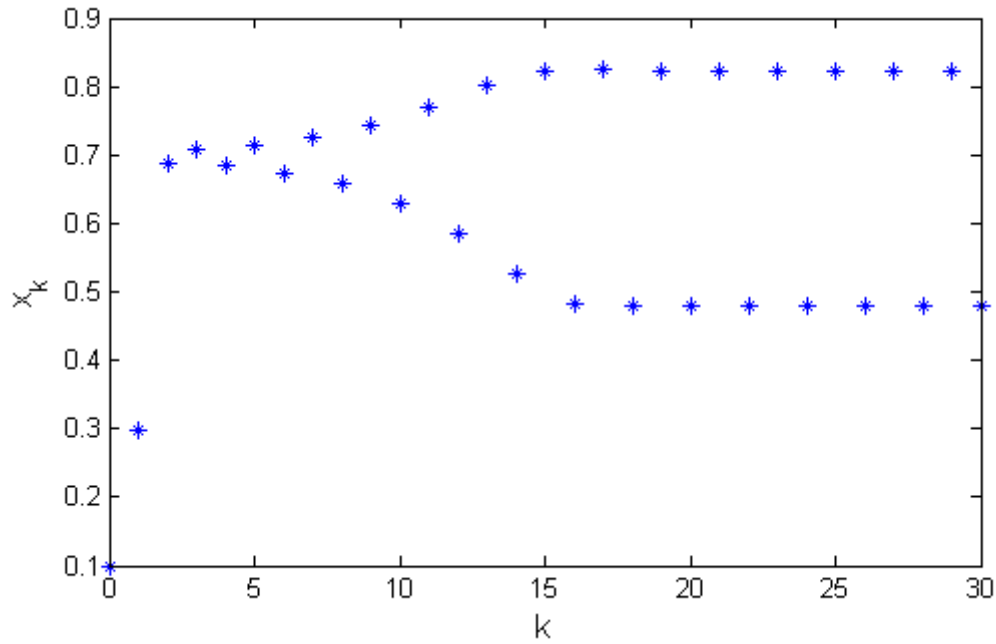


Figure 2.10: Solution of the logistic map for  $\mu = 3.3$ .

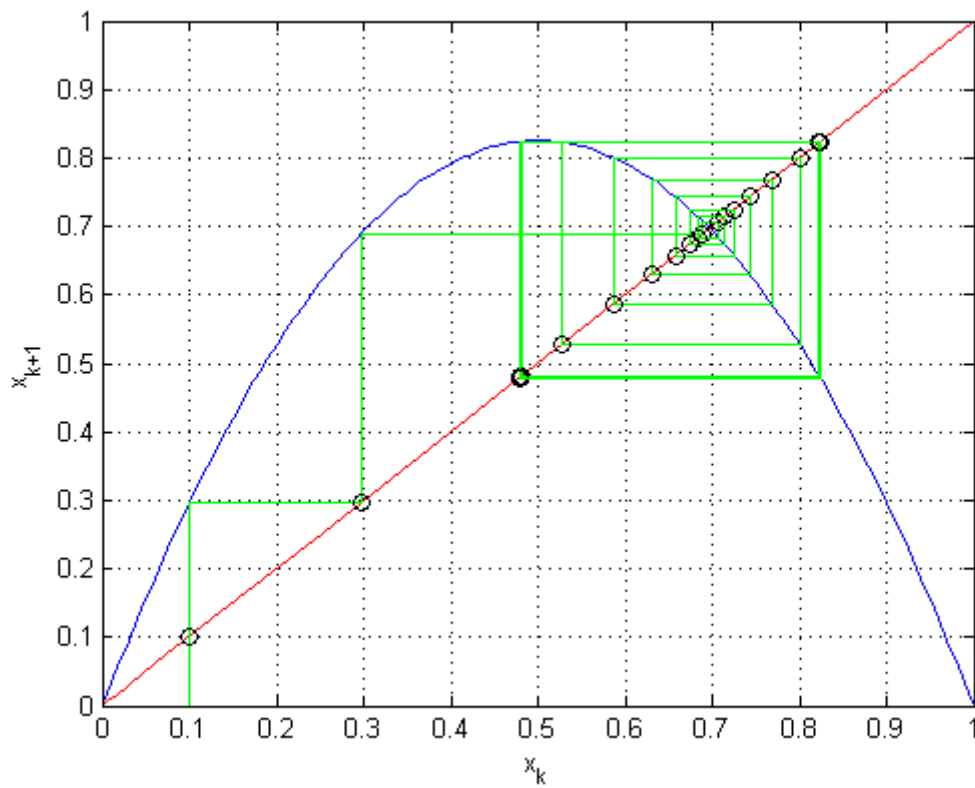
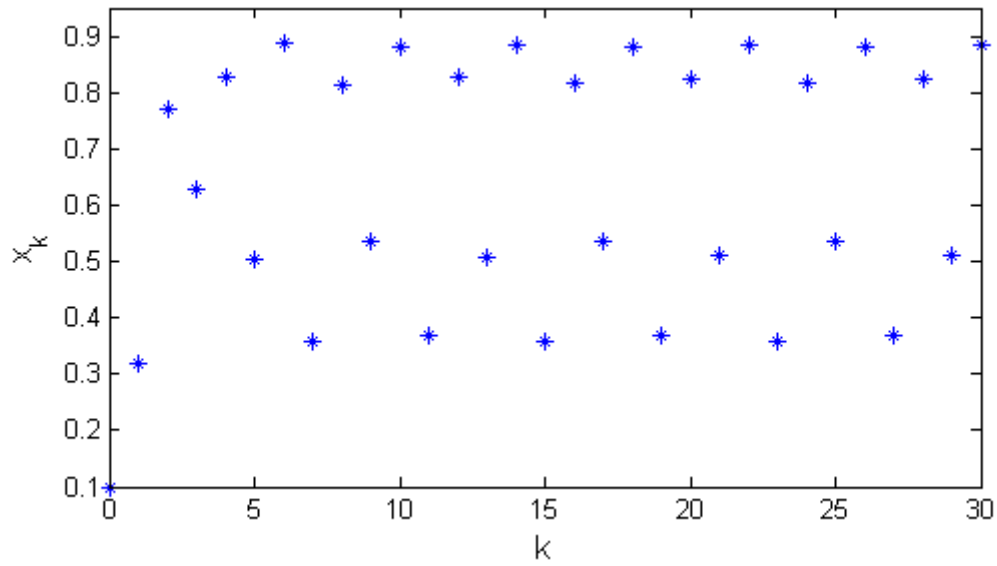
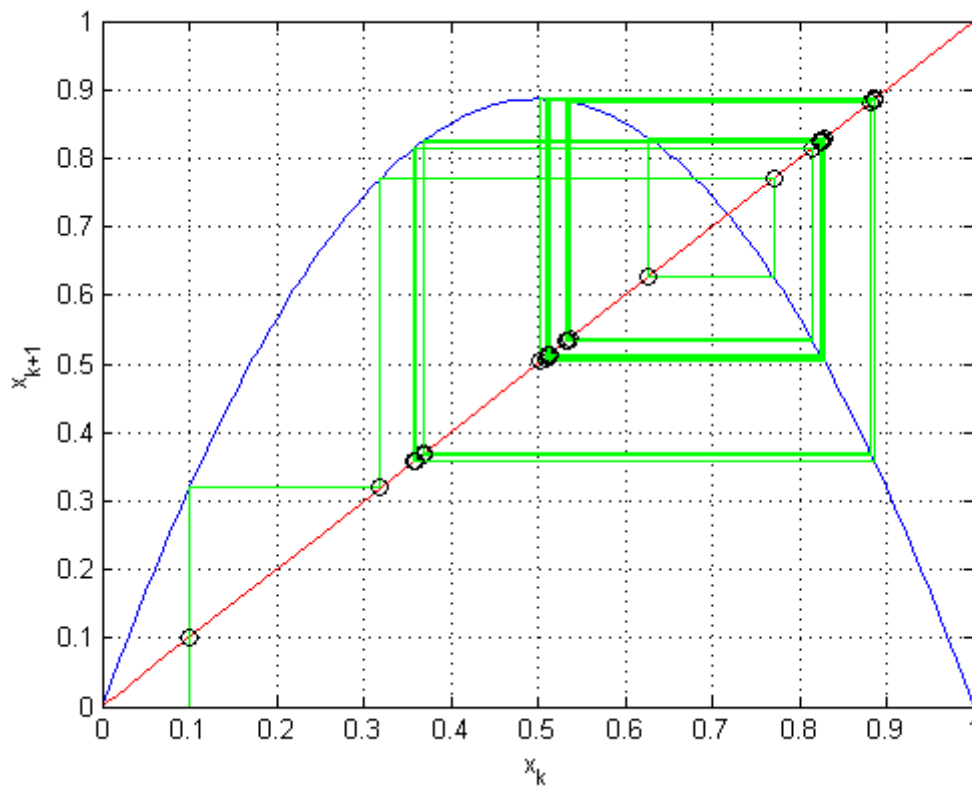


Figure 2.11: Cobweb diagram for the logistic map for  $\mu = 3.3$ .

When  $\mu$  increases beyond the value  $1 + \sqrt{6}$ , population oscillates between 4 values (see Figure 2.12 and 2.13), then 8, 16, 32 etc. This situation when the system switches to a new behaviour with twice the period of the original system is called period-doubling cascade.

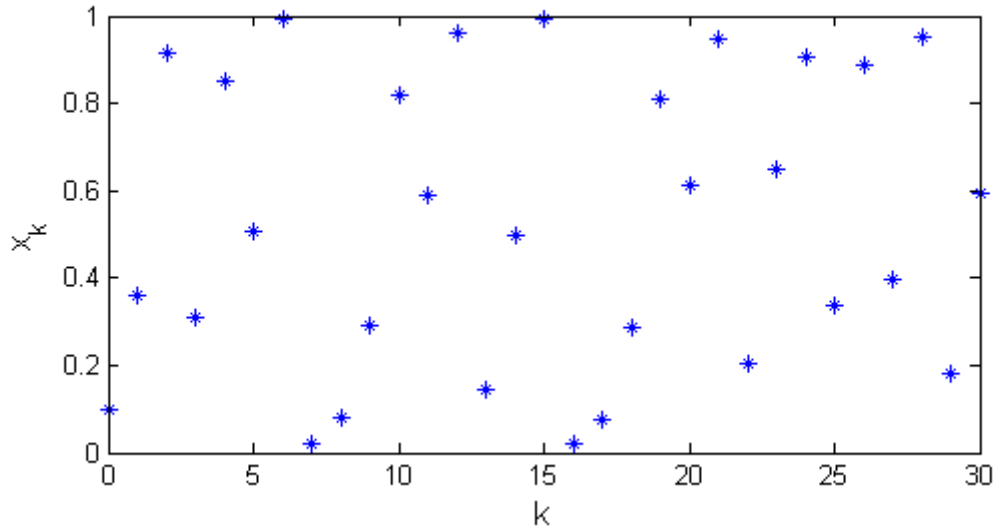


**Figure 2.12:** Solution of the logistic map for  $\mu = 3.545$ .

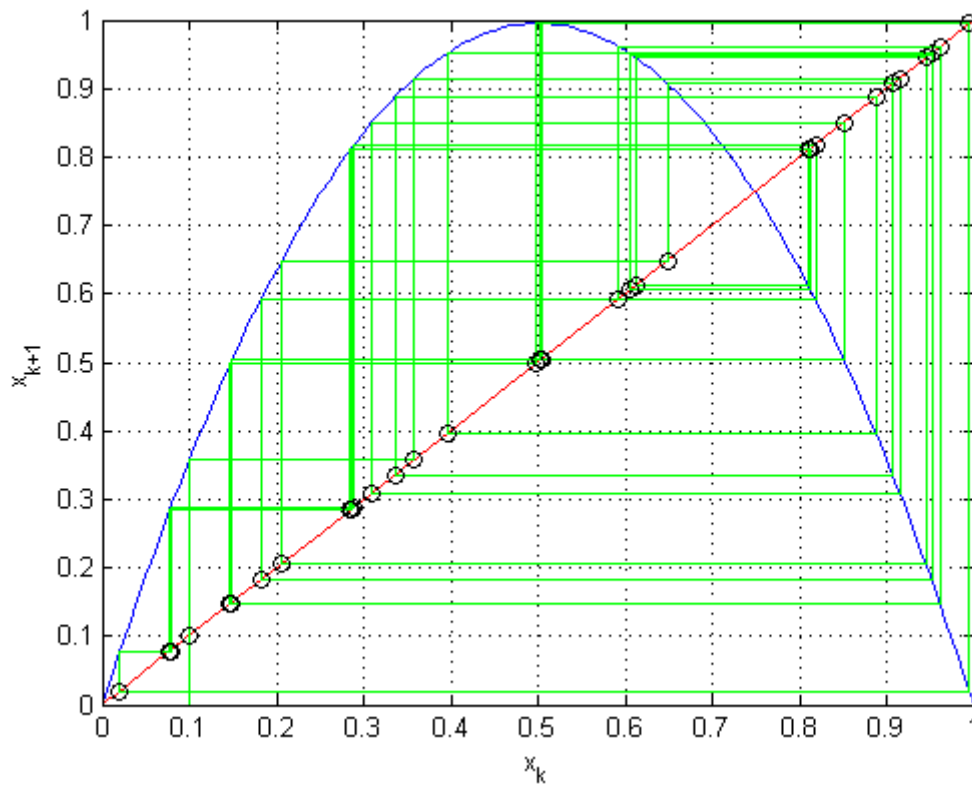


**Figure 2.13:** Cobweb diagram for the logistic map for  $\mu = 3.545$ .

The period-doubling cascade ends at value  $\mu \approx 3.57$  and the chaos begins. From almost all initial conditions we can no longer see any oscillation, the behaviour becomes chaotic (see Figure 2.14 and 2.15) and starts to be very sensitive to initial value which is a prime characteristic of chaos.



**Figure 2.14:** Solution of the logistic map for  $\mu = 3.98$ .



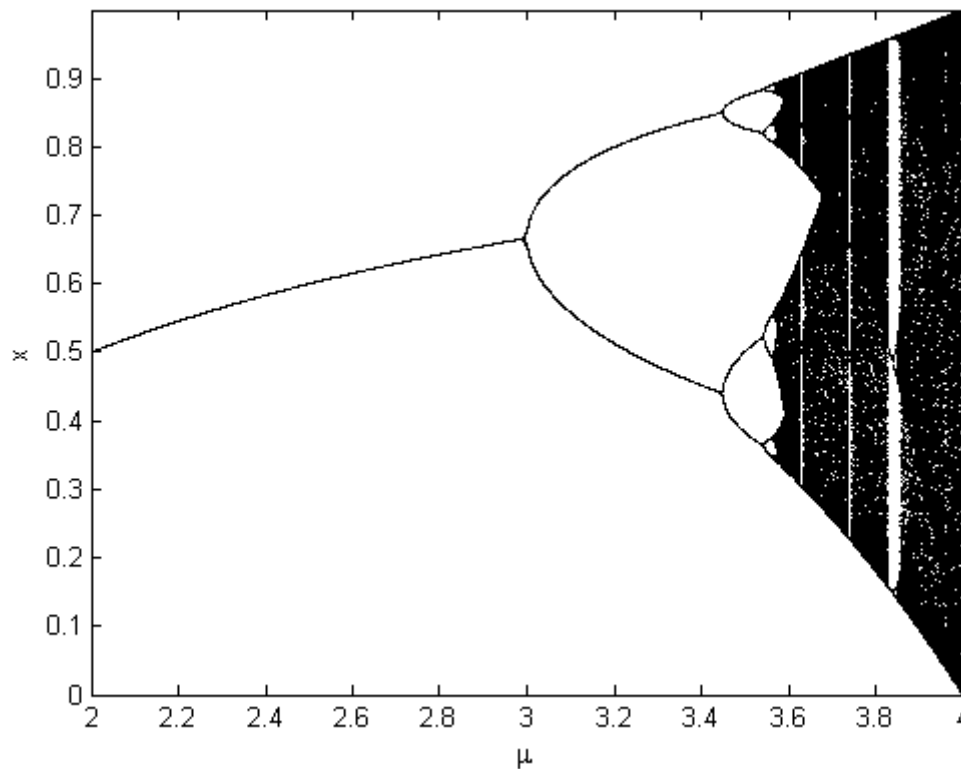
**Figure 2.15:** Cobweb diagram for the logistic map for  $\mu = 3.98$ .

Beyond the value  $\mu \approx 3.57$ , there are so called islands of stability, the isolated ranges of  $\mu$  that show non-chaotic behaviour. However, for the most values of  $\mu$  the behaviour stays chaotic.

If  $\mu$  varies from approximately 3.5699 to approximately 3.8284, the periodic phase are interrupted by bursts of aperiodic behaviour. This development of the chaotic behaviour is sometimes called Pomeau-Manneville scenario.

If  $\mu > 4$ , population diverges for almost all initial values.

The illustration below (Figure 2.16) shows the *bifurcation diagram* of the logistic map which summarizes its complex behaviour (we have used a code <sup>4</sup> in software Matlab for simulation the bifurcation diagram). In general, bifurcation diagram shows dependence of limit states (equilibria, fixed points) of a system on some parameter. It display some characteristic property of the asymptotic solution of a dynamical system allowing us to see where qualitative changes in the asymptotic solution occur. Such changes are termed bifurcations (see for example Section 2.1 in lecture notes from the Drexel University <sup>5</sup>).



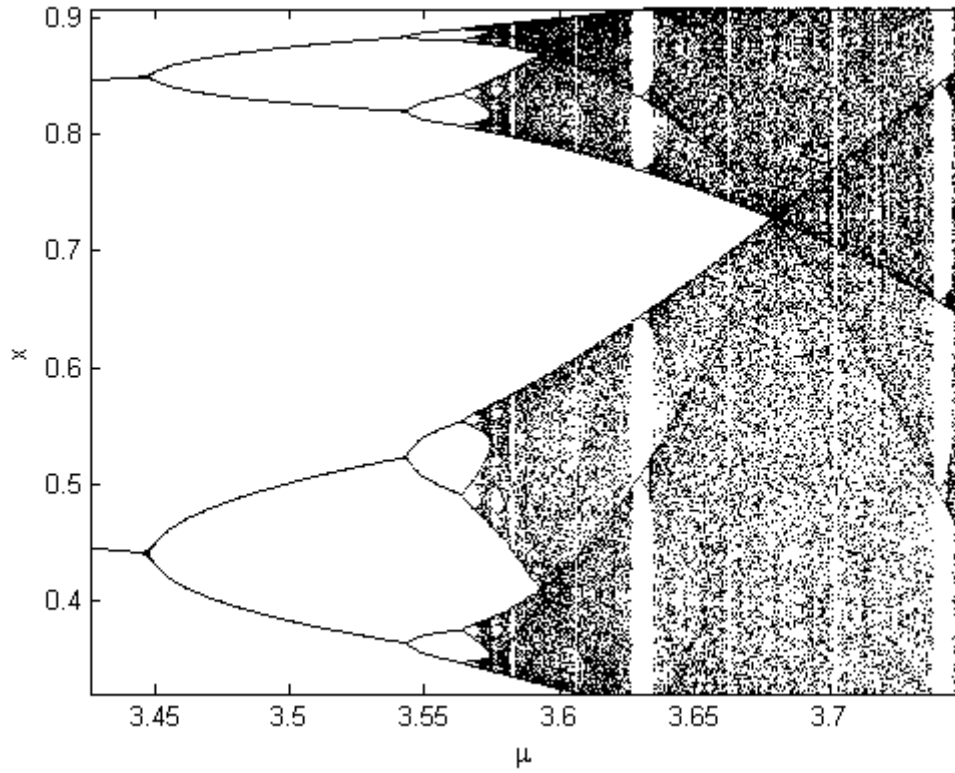
**Figure 2.16:** Bifurcation (Feigenbaum) diagram for the logistic map.

The bifurcation diagram is a self-similar: if we zoom in (see Figure 2.17) and focus on one arm of the three, the situation looks like a distorted version of the whole diagram <sup>5</sup>. Also the period-doubling cascade is better visible: until the value  $1 + \sqrt{6}$  which is

<sup>4</sup><http://www.mathworks.com/matlabcentral/fileexchange/32424-logistics-map>

<sup>5</sup>[http://en.wikipedia.org/wiki/Logistic\\_map](http://en.wikipedia.org/wiki/Logistic_map)

approximately 3.45, the population oscillates between two values, from approximately 3.45 to approximately 3.54 it oscillates between four values etc. Below we can see the enlargement of previous diagram about  $\mu = 3.6$ .



**Figure 2.17:** Enlargement of the bifurcation diagram for the logistic map.

## Chapter 3

# Stochastic Growth Models

Stochastic modelling is a technique of presenting data or predicting outcomes. It's based on probability theory therefore it takes into account a certain degree of randomness, or unpredictability.

Stochastic model incorporates one or several random variables to predict future conditions and to see what they might be like. It is possible to simulate processes with various parameters and observe estimated behaviour of a real system. Of course, the possibility of one random variable implies that many could occur. For this reason, stochastic models are run hundreds or even thousands of times. This larger collection of data not only expresses which outcomes are most likely, but what ranges can be expected as well. Stochastic model approximates real processes. Obviously it does not correspond exactly to real situations but it conforms with certain probability.<sup>1</sup>

For stochastic modelling we assume population size to be a random integer variable depending on time. Set of random variables creates random process. In this chapter we focus on models describing population size evolution using Markov chains. Both continuous and discrete-time models will be considered.

In this chapter we use the following sources: Fundamentals of random processes [11] written by Prášková and Lachout, bachelor thesis [6] written by V. Kulhavý and the article [1] written by L.J.S. Allen and E.J. Allen.

### 3.1 Continuous-time Markov Chain Models

**Definition 3.1.1.**  $(X_t, t \geq 0)$  is a *continuous-time Markov Chain* if it is a stochastic process taking values on a finite or countable set  $S$  with the Markov property that

$$\mathbf{P}(X_t = j \mid X_s = i, X_{t_n} = i_n, \dots, X_{t_1} = i_1) = \mathbf{P}(X_t = j \mid X_s = i) \quad (3.1)$$

$\forall i, j, i_1, \dots, i_n \in S \forall 0 \leq t_1 < t_2 < \dots < t_n < s < t : \mathbf{P}(X_s = i, X_{t_n} = i_n, \dots, X_{t_1} = i_1) > 0$ . We usually consider  $S \subseteq \mathbb{Z}$ ,  $S \subseteq \mathbb{N}_0$ ,  $S = \{0, 1, 2, \dots, k\}$ , etc.

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<sup>1</sup><http://www.wisegeek.com/what-is-stochastic-modeling.htm>

The changes of state of the system are called transitions, and the probabilities associated with various state-changes are called *transition probabilities*<sup>2</sup>. We denote them

$$p_{ij}(s, t) = \mathbf{P}(X_t = j | X_s = i) \quad (3.2)$$

and we say that  $p_{ij}(s, t)$  are transition probabilities from state  $i$  at time  $s$  to state  $j$  at time  $t$ . Probabilities  $p_j(t)$  defined as  $p_j(t) = \mathbf{P}(X_t = j)$ ,  $j \in S$  are called *absolute probabilities* at time  $t$  ([11], Chapter 3).

**Definition 3.1.2.** For every state  $i, j \in S$  we define *transition rate* from state  $i$  to state  $j$  at time 0 as

$$q_{ij} = \lim_{h \rightarrow 0_+} \frac{p_{ij}(h)}{h} \geq 0 \quad (3.3)$$

and

$$q_{ii} = -q_i; \quad q_i := \lim_{h \rightarrow 0_+} \frac{1 - p_{ii}(h)}{h} \geq 0. \quad (3.4)$$

Then  $Q = (q_{ij}, i, j \in S)$  is called *transition rate matrix*.

### 3.1.1 General Process of Growth

The general process of growth is a special case of continuous time Markov process where the states represent the current size of population. This population consists of individuals that act independently, they can reproduce but they can not die. Also no individual can migrate into the population. Population growth rate  $\lambda_j$  is not directly proportional to its current size.

#### Definition and Basic Properties

Let  $X_t$  be the population size (a number of individuals that occur in the population) at some time  $t$  and  $X_0 = i_0$  be the initial population size. Population size at time  $t \geq 0$  is described as a continuous time Markov chain  $(X_t, t \geq 0)$  with countable state space  $S$ , initial distribution  $p_{i_0}(0) = 1$ ,  $p_j(0) = 0$ ,  $j > i_0$  ( $i_0 \geq 0$ ) and transition rates

$$\begin{aligned} q_{j,j+1} &= \lambda_j \text{ for } j \geq i_0, \\ q_{jk} &= 0 \text{ otherwise } (k \neq j). \end{aligned}$$

This chain is called a *general process of growth*.

Transition rate matrix is

$$Q = \begin{pmatrix} -\lambda_{i_0} & \lambda_{i_0} & 0 & 0 & \dots \\ 0 & -\lambda_{i_0+1} & \lambda_{i_0+1} & 0 & \dots \\ 0 & 0 & -\lambda_{i_0+2} & \lambda_{i_0+2} & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix},$$

---

<sup>2</sup>[http://en.wikipedia.org/wiki/Markov\\_chain](http://en.wikipedia.org/wiki/Markov_chain)



where growth rates  $\lambda_j > 0$  reflect general dependence on current state  $j$  of the population (the states are numbered from  $j = i_0$ ) ([11], Section 3.6).

Absolute probabilities  $P(X_t = p_j(t))$  must satisfy Kolmogorov system of differential equations

$$\begin{aligned} p'_{i_0}(t) &= -\lambda_{i_0} p_{i_0}(t), \\ p'_j(t) &= \lambda_{j-1} p_{j-1}(t) - \lambda_j p_j(t), \quad j > i_0 \end{aligned}$$

with initial condition  $p_{i_0}(0) = 1$  ([11], Section 3.6). We are going to solve these equations.

We use separation of variables to solve the first differential equation.

$$\begin{aligned} p'_{i_0}(t) &= -\lambda_{i_0} p_{i_0}(t) \\ \frac{dp_{i_0}}{dt} &= -\lambda_{i_0} p_{i_0}(t) \\ \int \frac{dp_{i_0}}{p_{i_0}(t)} &= -\lambda_{i_0} \int dt \\ \ln(p_{i_0}(t)) &= -\lambda_{i_0} t + c, & c = c_2 - c_1 \\ \ln(p_{i_0}(t)) &= \ln(ke^{-\lambda_{i_0} t}), & c = \ln(k) \\ p_{i_0}(t) &= ke^{-\lambda_{i_0} t} \end{aligned}$$

We determine  $k = 1$  by substitution of initial condition. Therefore

$$p_{i_0}(t) = e^{-\lambda_{i_0} t}. \quad (3.5)$$

Then we solve this system recurrently.

$$\begin{aligned} p'_{i_0+1}(t) &= \lambda_{i_0} p_{i_0}(t) - \lambda_{i_0+1} p_{i_0+1}(t) \\ p'_{i_0+1}(t) + \lambda_{i_0+1} p_{i_0+1}(t) &= \lambda_{i_0} e^{-\lambda_{i_0} t} \end{aligned}$$

First we search for a solution of homogeneous differential equation

$$p'_{i_0+1}(t) + \lambda_{i_0+1} p_{i_0+1}(t) = 0, \quad (3.6)$$

and we get

$$p_{i_0+1}(t) = ce^{-\lambda_{i_0+1} t}. \quad (3.7)$$

Next we use variation of parameters (variation of constants) method for finding a partic-

ular solution.

$$\begin{aligned}
 p_{i_0+1}(t) &= ce^{-\lambda_{i_0+1}t} \\
 p'_{i_0+1}(t) &= c'(t)e^{-\lambda_{i_0+1}t} - \lambda_{i_0+1}c(t)e^{-\lambda_{i_0+1}t} \\
 c'(t) &= e^{-\lambda_{i_0+1}t} \\
 c'(t) &= \lambda_{i_0}e^{-\lambda_{i_0}t} \\
 c'(t) &= \lambda_{i_0}e^{-(\lambda_{i_0}+\lambda_{i_0+1})t} \\
 c(t) &= \frac{\lambda_{i_0}}{-\lambda_{i_0} + \lambda_{i_0+1}} e^{-(\lambda_{i_0}-\lambda_{i_0+1})t}
 \end{aligned}$$

We substitute initial condition and we obtain  $c = \frac{\lambda_{i_0}}{\lambda_{i_0} - \lambda_{i_0+1}}$ . Thus the formula is in the following form

$$p_{i_0+1}(t) = \frac{\lambda_{i_0}}{\lambda_{i_0} - \lambda_{i_0+1}} e^{-\lambda_{i_0+1}t} + \frac{\lambda_{i_0}}{\lambda_{i_0} - \lambda_{i_0+1}} e^{-\lambda_{i_0}t}. \quad (3.8)$$

The particular solution of non-homogeneous differential equation is

$$p_{i_0+1}(t) = \lambda_{i_0} e^{-\lambda_{i_0}t} \int_0^t e^{\lambda_{i_0+1}s} p_{i_0}(s) ds. \quad (3.9)$$

In general:

$$p_j(t) = \lambda_{j-1} e^{-\lambda_j t} \int_0^t e^{\lambda_j s} p_{j-1}(s) ds, \quad j > i_0. \quad (3.10)$$

Finally, by solving this system we determine absolute probabilities recurrently by

$$\begin{aligned}
 p_{i_0}(t) &= e^{-\lambda_{i_0}t}, \\
 p_j(t) &= \lambda_{j-1} e^{-\lambda_j t} \int_0^t e^{\lambda_j s} p_{j-1}(s) ds, \quad j > i_0.
 \end{aligned}$$

**Definition 3.1.3.** Homogeneous Markov chain with stable states is called *regular* if

$$P_i(\xi = \infty) = 1, \quad \forall i \in S, \quad (3.11)$$

where random variable  $\xi$  is called the explosion time and it is defined as  $\xi = \sum_{k=1}^{+\infty} s_k$ , where  $s_k$  are time periods between particular transitions.

In other words, process is regular if only finite number of transitions between states of the chain occurs on every finite interval  $(0, t)$  with probability equal to one ([11], Section 3.1).

**Lemma 3.1.1.** General growth process is regular if and only if

$$\sum_{j=i_0}^{\infty} \frac{1}{\lambda_j} = \infty. \quad (3.12)$$

*Proof.*  $\forall i_0 \geq 0 : P_{i_0}(Y_n = n + i_0) = 1$  for relevant nested chain  $Y_n$  ([11], Section 3.6).  $\square$

### Stationary distribution

**Definition 3.1.4.** Markov chain is called *irreducible* if its state space is a single communicating class; in other words, if it is possible to get to any state from any state.<sup>3</sup> ([11], Section 2.4)

**Definition 3.1.5.** [11] Let  $(X_t, t \geq 0)$  be a continuous-time Markov chain with state space  $S$  and transition matrix  $P$ . A (row) vector  $\pi = \{\pi_j, j \in S\}$  with  $\pi_j \geq 0$  for all  $j$  and  $\sum_{j \in S} \pi_j = 1$ , is said to be a *stationary distribution* if

$$\pi^T = \pi^T P, \quad (3.13)$$

or

$$\pi_j = \sum_{k \in S} \pi_k p_{kj}, \quad j \in S. \quad (3.14)$$

Vector  $\pi$  which satisfies (3.13) is called a stationary distribution because it makes the process stationary. That is, if we set the initial distribution of  $X_0$  to be such a  $\pi$ , then the distribution of  $X_t$  will also be  $\pi$  for all  $t > 0$ .

**Lemma 3.1.2.** Let  $X(t)$  be a regular general process of growth and let this chain be irreducible. Denote

$$\begin{aligned} \rho_0 &= 1 \\ \rho_N &= \frac{\lambda_{i_0}}{\lambda_{i_0+N}}, \quad N = 1, 2, \dots \end{aligned}$$

Let

$$\sum_{N=0}^{\infty} \rho_N = \sum_{N=0}^{\infty} \frac{\lambda_{i_0}}{\lambda_{i_0+N}} = \lambda_{i_0} \sum_{N=0}^{\infty} \frac{1}{\lambda_{i_0+N}} < \infty. \quad (3.15)$$

Then there is exactly one stationary distribution of the process  $X(t)$  in following formula

$$\pi_N = \rho_N \left( \sum_{N=0}^{\infty} \rho_N \right)^{-1}, \quad N = 0, 1, \dots \quad (3.16)$$

*Proof.* Let  $X(t)$  be regular, irreducible general process of growth and let  $\sum_{N=0}^{\infty} \rho_N < \infty$ . Let's find invariant measure  $\eta$  such as

$$\eta^T Q = 0^T. \quad (3.17)$$

For transition rate matrix of general growth process we obtain these equations from the formula above

$$\begin{aligned} -\lambda_{i_0} \eta_0 &= 0 \\ -\lambda_{i_0+N} \eta_N + \lambda_{i_0+(N-1)} \eta_{N-1} &= 0 \end{aligned}$$

for  $N = 1, 2, \dots$ . From the second equation we can express  $\eta_N$ :

$$\eta_N = \frac{\lambda_{i_0+(N-1)}}{\lambda_{i_0+N}} \eta_{N-1} = \frac{\lambda_{i_0+(N-1)} \lambda_{i_0+(N-2)}}{\lambda_{i_0+N} \lambda_{i_0+(N-1)}} \eta_{N-2} = \frac{\lambda_{i_0}}{\lambda_{i_0+N}} \eta_0 = \rho_N \eta_0. \quad (3.18)$$

<sup>3</sup>[http://en.wikipedia.org/wiki/Markov\\_chain](http://en.wikipedia.org/wiki/Markov_chain)

Obviously, stationary distribution exists if  $\sum_{N=0}^{\infty} \rho_N < \infty$ , therefore

$$\sum_{N=0}^{\infty} \frac{\lambda_{i_0}}{\lambda_{i_0+N}} < \infty, \quad (3.19)$$

and is equal to

$$\pi_N = \rho_N \left( \sum_{N=0}^{\infty} \rho_N \right)^{-1}, \quad N = 0, 1, \dots \quad (3.20)$$

The solution is unique because of the irreducibility of the chain.  $\square$

The principle above is based on deduction of stationary distribution of general birth and death process ([6], Subsection 3.2.1).

### Generating function

We have already found the absolute probabilities by using the Kolmogorov differential equations. Another way how to find these probabilities is using generating function method. Consider generating function with this distribution  $\{p_j(t), j \in N_0\}$ ,

$$\pi(s, t) = \sum_{j=0}^{\infty} p_j(t) s^j \quad (3.21)$$

as a function of two variables  $s, t$  ([11], Section 3.4). Then

$$\begin{aligned} \frac{\partial \pi}{\partial t}(s, t) &= \sum_{j=0}^{\infty} p'_j(t) s^j \\ \frac{\partial \pi}{\partial s}(s, t) &= \sum_{j=1}^{\infty} j p_j(t) s^{j-1} \\ \pi(s, 0) &= \sum_{j=0}^{\infty} p_j(0) s^j = p_{i_0}(0) s^{i_0} = s^{i_0}. \end{aligned}$$

From Kolmogorov differential equations

$$\begin{aligned} p'_{i_0}(t) &= -\lambda_{i_0} p_{i_0}(t), \\ p'_j(t) &= \lambda_{j-1} p_{j-1}(t) - \lambda_j p_j(t), \quad j > i_0 \end{aligned}$$

we obtain

$$\sum_{j=2}^{\infty} p'_j(t) s^j = \sum_{j=2}^{\infty} (\lambda_{j-1} p_{j-1}(t) s^j - \lambda_j p_j(t) s^j) = \sum_{j=2}^{\infty} \lambda_{j-1} p_{j-1}(t) s^j - \sum_{j=2}^{\infty} \lambda_j p_j(t) s^j. \quad (3.22)$$

Unfortunately, it is possible to express the searched absolute probabilities from this formula only in special cases, in particular in a linear case.

### Linear Growth Process (Yule Process)

A special case of general growth process is *linear growth process* also called *Yule process*. It is a birth process based on the assumption of independence and of constant birth rate. We assume that each individual gives birth to a new one in interval  $(t, t+h]$  with probability  $\lambda h + o(h)$  (to no one with probability  $1 - \lambda h + o(h)$ ,  $\lambda > 0$ .) Then the transition probabilities are

$$\begin{aligned} p_{j,j+1}(h) &= \binom{j}{1}(\lambda h + o(h))(1 - \lambda h + o(h))^{j-1} = j\lambda h + o(h) \\ p_{j,j+k}(h) &= o(h) \quad k \geq 2 \\ p_{jj}(h) &= (1 - \lambda h + o(h))^j = 1 - j\lambda h + o(h) \\ p_{jk} &= 0 \quad \text{otherwise.} \end{aligned}$$

The transition rates are

$$\begin{aligned} q_{j,j+1} &= j\lambda \\ q_j &= j\lambda \\ q_{jk} &= 0 \quad \text{otherwise,} \end{aligned}$$

thus the transition rate matrix is

$$\mathbf{Q} = \begin{pmatrix} -\lambda & \lambda & 0 & 0 & \dots \\ 0 & -2\lambda & 2\lambda & 0 & \dots \\ 0 & 0 & -3\lambda & 3\lambda & \dots \\ \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix}.$$

We suppose the initial condition  $p_1(0) = 1, p_j(0) = 0, j > 1$ . Absolute probabilities must satisfy Kolmogorov differential equations system

$$\begin{aligned} p_1'(t) &= -\lambda p_1(t) \\ p_j'(t) &= \lambda j p_j(t) + \lambda(j-1)p_{j-1}(t), \quad j > 1 \end{aligned}$$

with initial condition  $p_1(0) = 1$  ([11], Section 3.5). This system of differential equations can be solved by generating function method.

We multiple the system by  $s^j$  and get

$$\begin{aligned} \sum_{j=1}^{+\infty} p_j'(t)s^j &= -\lambda \sum_{j=1}^{+\infty} j p_j(t)s^j + \lambda \sum_{j=1}^{+\infty} (j-1)p_{j-1}(t)s^j \\ \sum_{j=1}^{+\infty} p_j'(t)s^j &= -\lambda \sum_{j=1}^{+\infty} j p_j(t)s^j + \lambda \sum_{j=1}^{+\infty} j p_j(t)s^{j+1} \end{aligned}$$

which we can write as a partial differential equation(PDE)

$$\frac{\partial \pi}{\partial t}(s, t) = -\lambda s \frac{\partial \pi}{\partial s}(s, t) + \lambda s^2 \frac{\partial \pi}{\partial s}(s, t) = \lambda s(s-1) \frac{\partial \pi}{\partial s}(s, t). \quad (3.23)$$

We solve this PDE and obtain its solution

$$\pi(s, t) = \sum_{j=1}^{+\infty} p_j(t) s^j = \frac{se^{-\lambda t}}{1 - (s + se^{-\lambda t})}. \quad (3.24)$$

Next we use this formula  $\frac{a_0}{1-q} = \sum_{j=0}^{+\infty} a_0 q^j$  and adjust the equation

$$\begin{aligned} \frac{se^{-\lambda t}}{1 - (s + se^{-\lambda t})} &= se^{-\lambda t} \sum_{j=0}^{+\infty} (s + se^{-\lambda t})^j \\ e^{-\lambda t} \sum_{j=0}^{+\infty} (1 - e^{-\lambda t})^j s^{j+1} &= \sum_{j=0}^{+\infty} e^{-\lambda t} (1 - e^{-\lambda t})^{j-1} s^j. \end{aligned}$$

Because this result is equal to  $\sum_{j=1}^{+\infty} p_j(t) s^j$ , we can say that the solution of the Kolmogorov differential equation system are the absolute probabilities

$$p_j(t) = e^{-\lambda t} (1 - e^{-\lambda t})^{j-1}, \quad j \geq 1. \quad (3.25)$$

We can easily verify that sum of these probabilities is equal to one for every  $t \geq 0$ :

$$\sum_{j=1}^{+\infty} p_j(t) = \frac{e^{-\lambda t}}{1 - (1 - e^{-\lambda t})} = 1. \quad (3.26)$$

Population mean at time  $t$  is

$$E(X_t) = \sum_{j=1}^{+\infty} j p_j(t) = e^{\lambda t}. \quad (3.27)$$

### 3.1.2 Stochastic Logistic Growth Model

We evolve the stochastic logistic growth model from the general growth model by taking

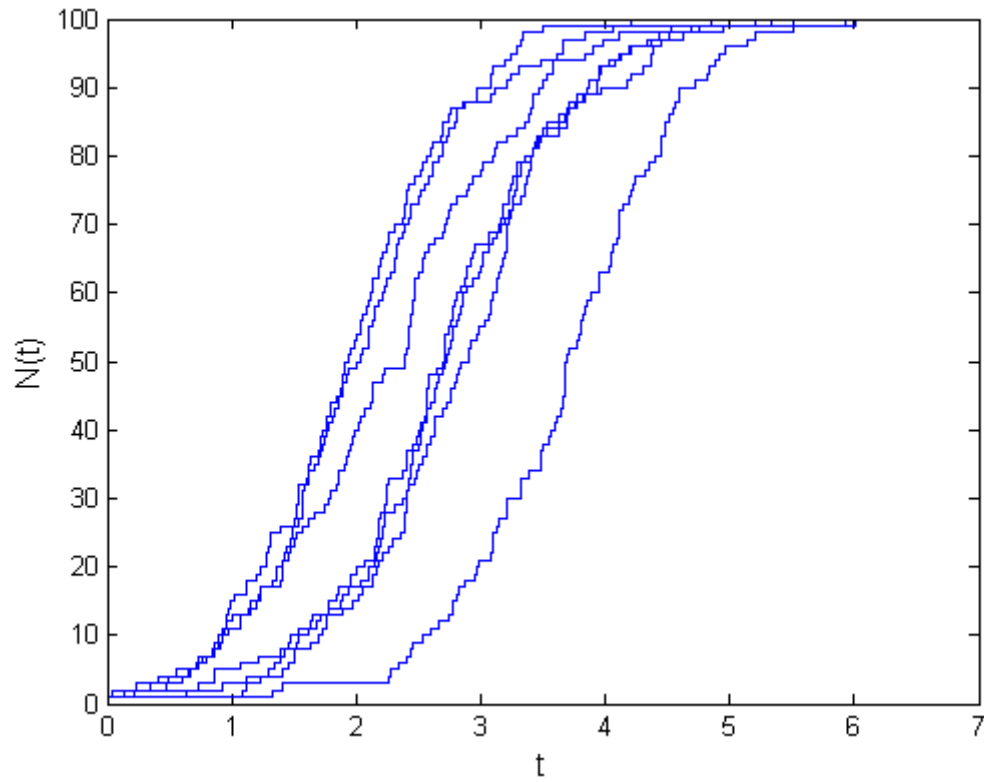
$$\lambda_{i_0+N} = b_1 N(t) - b_2 N(t)^2, \quad (3.28)$$

where  $N(t)$  is the population size at time  $t$  and  $b_1, b_2$  are positive parameters ([6], Section 4.2).

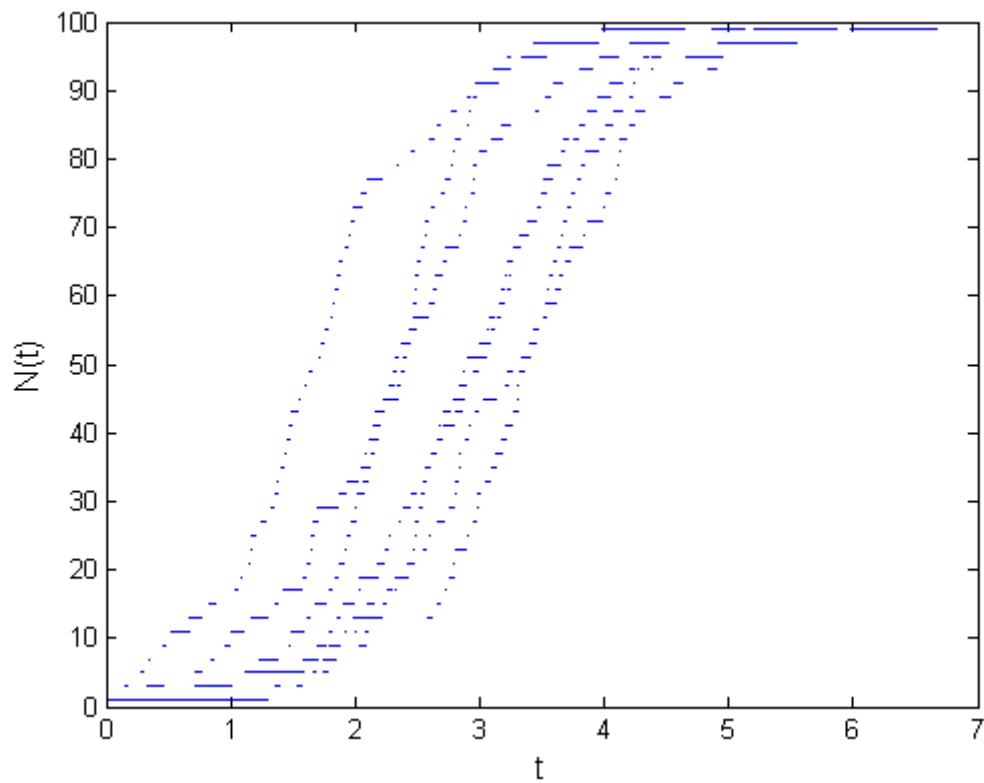
We can see simulation of the example for concrete parameters  $b_1 = 2, b_2 = 0.02$  in Figure 3.1 and 3.2 (simulations were done by modifying the original source code<sup>4</sup> written by R.Gaigalas and I.Kajin in software Matlab). There are seven randomly generated paths in these graphs which represent stochastic solutions.

In Figure 3.1 there are vertical abscissas which have been caused by time jumps. Actually they are not a part of the simulated solution and are illustrated for convenience only. The trajectories of continuous-time Markov chains are piecewise constant functions as described in Figure 3.2.

<sup>4</sup><http://www.mathworks.com/matlabcentral/fileexchange/2493-simulation-of-stochastic-processes/content/stproc/birthdeath.m>



**Figure 3.1:** Simulation of stochastic logistic growth for parameters  $b_1 = 2$ ,  $b_2 = 0.02$ .



**Figure 3.2:** Modified simulation of stochastic logistic growth for parameters  $b_1 = 2$ ,  $b_2 = 0.02$ .

## 3.2 Discrete-time Markov Chain Models

**Definition 3.2.1.**  $(X_n; n \in N_0)$  is a *discrete-time Markov Chain* if it is a discrete time stochastic process with discrete state space  $S = \{0, 1, \dots, N\}$  and with the Markov property that

$$\mathbf{P}(X_{n+1} = j | X_0 = i_0, X_1 = i_1, \dots, X_n = i) = \mathbf{P}(X_{n+1} = j | X_n = i) \quad (3.29)$$

$$\forall n \in N_0 \forall i_0, i_1, \dots, i, j \in S : \mathbf{P}(X_0 = i_0, X_1 = i_1, \dots, X_n = i) > 0.$$

Conditional probabilities  $P(X_{n+1} = j | X_n = i) = p_{ij}(n, n+1)$  (if they are defined) are called transition probabilities from state  $i$  at time  $n$  to state  $j$  at time  $n+1$  ([11], Chapter 2).

### 3.2.1 General Process of Growth

Let  $X(t)$  denote the random variable for the population size at some time  $t$ . The population size is described by the discrete-time Markov chain with discrete state space  $S = \{0, 1, \dots, N\}$ <sup>5</sup>. Let  $\Delta t$  be a fixed time interval,  $t \in \{0, \Delta t, 2\Delta t, \dots\}$  and let  $\lambda_j > 0$  be the growth rate. Then a birth occurs with probability  $\lambda_j \Delta t$  and the transition probabilities  $p_{ij}(\Delta t)$  are

$$\begin{aligned} p_{j,j-1}(\Delta t) &= \lambda_j \Delta t, \quad j \in \{1, \dots, N\} \\ p_{j,j}(\Delta t) &= 1 - \lambda_j \Delta t, \quad j \in \{0, 1, \dots, N\} \\ p_{jk} &= 0, j \neq k \quad \text{otherwise.} \end{aligned}$$

This chain is called a discrete general process of growth.

Now  $p_j(t + \Delta t)$  satisfies the following difference equations

$$\begin{aligned} p_j(t + \Delta t) &= \lambda_{j-1} \Delta t p_{j-1}(t) + (1 - \lambda_j \Delta t) p_j(t) \quad \text{for } j = 1, 2, \dots, N-1 \\ p_0(t + \Delta t) &= p_0(t) \quad \text{for } j = 0 \\ p_N(t + \Delta t) &= \lambda_{N-1} \Delta t p_{N-1}(t) + p_N(t) \quad \text{for } j = N. \end{aligned}$$

The difference equations can be expressed in matrix form as

$$p(t + \Delta t) = P p(t), \quad p_{i_0} = 1, \quad (3.30)$$

where  $P = (p_{ij}(\Delta t))$  is the transition matrix in the following form

$$\mathbf{P} = \begin{pmatrix} 1 & 0 & 0 & 0 & \dots & 0 \\ 0 & 1 - \lambda_1 \Delta t & \lambda_1 \Delta t & 0 & \dots & 0 \\ 0 & 0 & 1 - \lambda_2 \Delta t & \lambda_2 \Delta t & \dots & 0 \\ 0 & 0 & 0 & 1 - \lambda_3 \Delta t & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \dots & \lambda_{N-1} \Delta t \\ 0 & 0 & 0 & 0 & \dots & 1 \end{pmatrix}.$$

<sup>5</sup>therefore both time and population size are discrete-valued



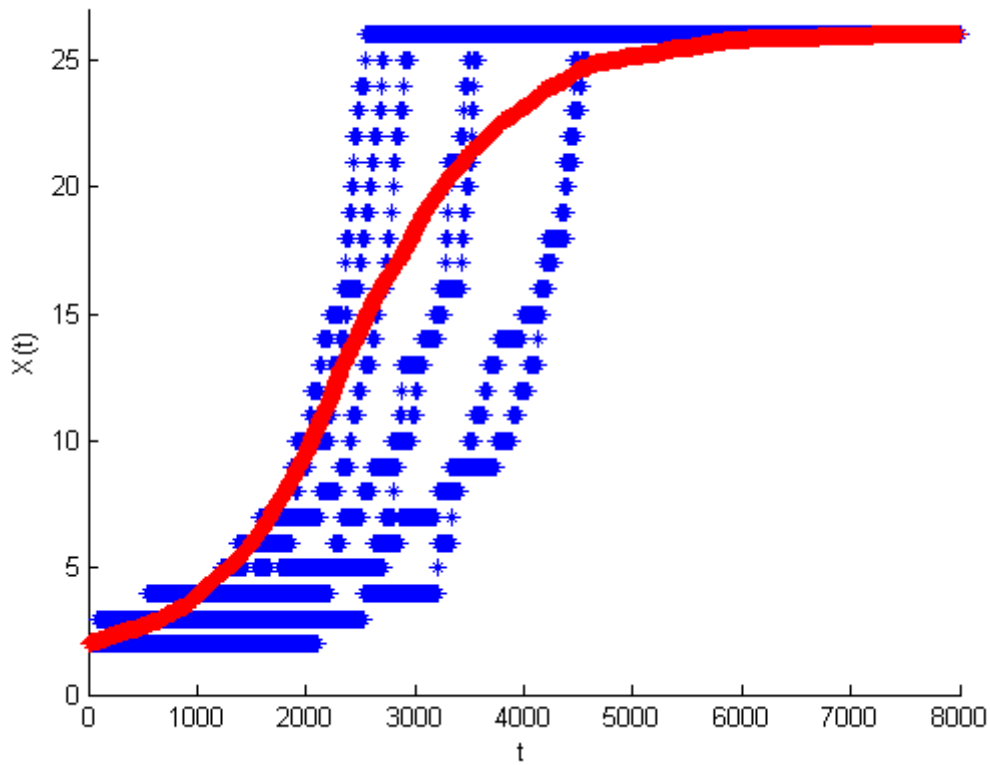
To ensure that  $P$  is a stochastic matrix (it means it is nonnegative and the column elements sum to one), it is assumed that

$$\max_{j \in \{1, 2, \dots, N\}} \{\lambda_j \Delta t\} \leq 1. \quad (3.31)$$

Information about stochastic birth and death process containing the discrete-time Markov chain model, continuous-time Markov chain model and more can be found in the article [1] written by L.J.S. Allen and E.J. Allen.

Since we know the transition matrix, we can simulate the discrete-time growth process. We can see the simulation for concrete parameters  $b_1 = 1$ ,  $b_2 = 0.02$  in the Figure 3.3 (simulations were done by modifying the original source code<sup>6</sup> written by Craig L. Zirbel in software Matlab).

For the initial population size  $i_0 = 2$ , there are seven randomly generated sequences in this graph which represent stochastic solutions, and the mean value represented by the red curve, which is determined from a hundred of randomly generated sequences.

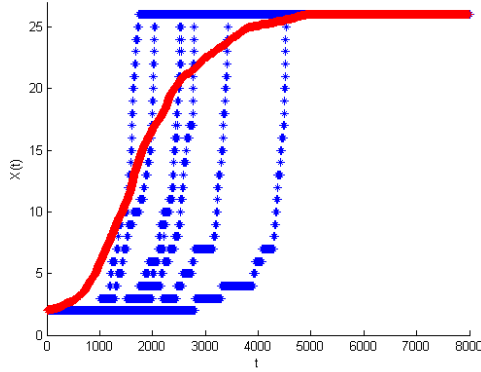
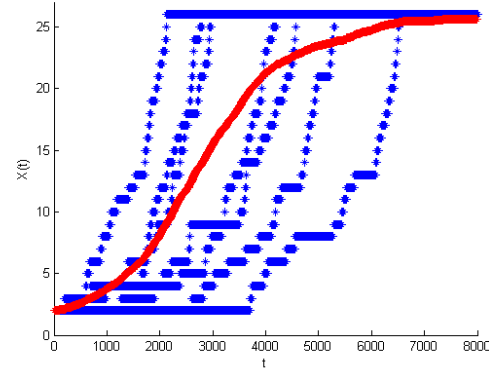


**Figure 3.3:** Simulation of discrete-time Markov Chain growth process for parameters  $b_1 = 1$ ,  $b_2 = 0.02$  and initial condition  $i_0 = 2$ .

In Figure 3.4 there are simulations for  $b_1 = 1$ ,  $b_2 = 0.2$  and  $b_1 = 1$ ,  $b_2 = 0.002$ . We can see what happen when we have  $b_1$  fixed and  $b_2$  is changing - if  $b_2$  is bigger the

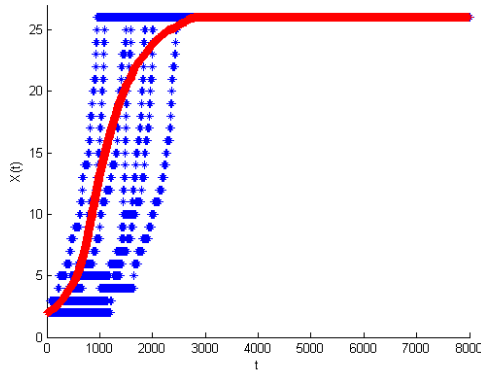
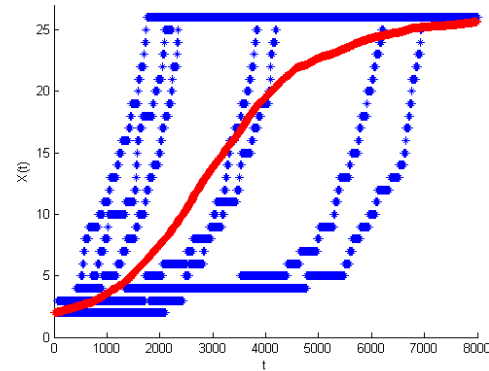
<sup>6</sup><http://www-math.bgsu.edu/~zirbel/ap/>

population grows faster, and conversely, if  $b_2$  is smaller the population growth slows down.

(a)  $b_2 = 0.2$ (b)  $b_2 = 0.002$ 

**Figure 3.4:** Simulation of discrete-time Markov Chain growth process for parameters  $b_1 = 1$ ,  $b_2 = 0.2/b_2 = 0.002$  and initial condition  $i_0 = 2$ .

Similar behaviour can be observed in Figure 3.5 only this time we change the parameter  $b_1$  while the second parameter  $b_2$  is fixed.

(a)  $b_1 = 2.5$ (b)  $b_2 = 0.8$ 

**Figure 3.5:** Simulation of discrete-time Markov Chain growth process for parameters  $b_1 = 2.5/b_1 = 0.8$ ,  $b_2 = 0.02$  and initial condition  $i_0 = 2$ .

## Chapter 4

# Conclusion

At the final chapter, we are going to summarize basic characteristics, advantages and disadvantages of the presented models and compare stochastic and deterministic models.

The first mentioned model was the logistic equation (or the logistic growth). It is a very simple model and its potential disadvantages are well known:

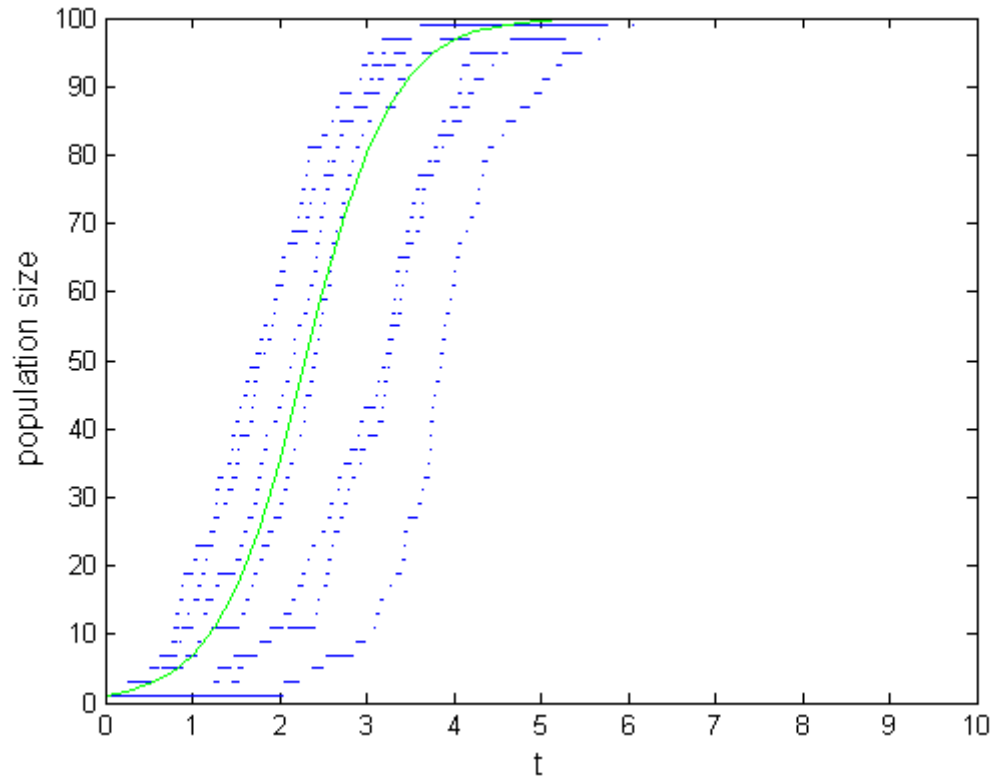
- (i) rate function  $r(t) = \frac{dN}{Ndt}$  is related to  $N$  linearly which means the first simplification,
- (ii) the rate of population change responds to variations in density instantaneously, i.e. there is no time lag like in the real world,
- (iii) the model does not incorporate the effects of external influences,
- (iv) it neglects effects of population structure.

In spite of these failings, the logistic model is taught by all ecology texts. The reason is that it provides a simple and powerful metaphor for a regulated population, and the reasonable starting point for modelling single-population dynamics. Moreover it can be modified to address all four criticisms listed above ([14], Subsection 3.1.1).

The second presented model was logistic map. Although we are dealing with very simple equation, the model is capable of very various and complex behaviour and at last this simple system will be seen to display many of the essential features of deterministic chaos.

Then we focused on stochastic models: continuous-time and discrete-time Markov Chain models. The main difference between these two approaches is that in the discrete-time model we are especially interested in the information about a number of individuals in the population in a concrete time while the continuous-time model also adds the information for how long the population stays in the particular state.

Finally, there is Figure 4.1 that compares the stochastic and the deterministic solution in the continuous time. Like in the Subsection 3.1.2 there are seven randomly generated functions which represent stochastic solutions and in addition there is the exact deterministic solution represented by the green line.



**Figure 4.1:** Comparison of stochastic and deterministic growth models. Simulation of stochastic logistic growth is for parameters  $b_1 = 2$ ,  $b_2 = 0.02$ , simulation of deterministic logistic growth is for parameters  $r = 2$ ,  $K = \frac{2}{0.02}$ .

# Appendix A

## Content of the CD attachment

The attached CD contains:

- Matlab - includes Matlab scripts used for the simulations presented in the thesis. Both original code cited in the text and modified versions are included.
- Latex - includes Latex files used for generating the thesis with all settings, graphics and bibliography.
- Thesis.pdf - the Bachelor thesis.
- README.txt - this text file.

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